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A case of bud-variation in Pelargonium

A. B. STOUT

(WITH PLATE 20)

The precise nature of bud-variation is not satisfactorily known. No adequate classification of the various kinds of bud-variation has been made. Recent investigations regarding the nature of plant chimeras indicate that some of the phenomena generally considered as bud-variation are associated with chimeras and are to be explained by the nature of the chimeras. Observations and experiments are now being made at the New York Botanical Garden on various types of bud-variation. In the studies on *Pelargonium* one case has arisen which seems of special interest in its bearing on the nature of bud-sports from plants that are chimeras.

Baur (1909 *a* and *b*; 1911) has recently shown that the variegation in the case of the "albomarginatae" varieties of *Pelargonium zonale* is due to the presence of white and green cells which are sharply distinct and which occupy a characteristic position in relation to each other. It has been long known that the paler tissue of these variegated plants owes its characteristics to a lack of chlorophyl in its cells. Baur shows that the plastids are present in the white cells but are colorless.

Baur further claims that this arrangement of green and white cells in the leaf can be explained by the arrangement of the corresponding tissues in the growing point and actually shows that in the plants whose leaves have layers of white cells on the exterior there is in the apex of the stem a cap of white cells over the greener cells beneath. In such plants the relative position of the white and the green cells is maintained throughout the development of the leaves.

By further study Baur (1909 *a*; 1911) found that in other cases these two kinds of cells may be variously arranged with reference to each other. In some plants various stems and leaves show a sectoral arrangement with a more or less bilateral distribution of the two kinds of cells. In certain types of *Pelargonium* the green cells are outside as one or two layers covering the white cells. In some individuals streaks of one of the tissues are mingled with the other.

Baur is able to interpret the conditions in these various forms by using the conception developed by Winkler (1907) in his remarkable discoveries regarding the so-called chimera-nature of graft hybrids. Baur introduced the term *periclinal chimera* for the condition where the peripheral cell-layers are different from the enclosed tissues and *sectoral chimera* for the cases where there is more or less of a bilateral or radial distribution. The term *hyperchimera*, first suggested by Strasburger (1909), is used for the cases where there is a more or less intimate mixture of the different kinds of cells.

On these various chimeras of *Pelargonium*, wholly green or wholly white shoots may arise. This is due to the fact that the two kinds of cells which are maintained by the cell divisions in the meristematic regions become segregated in the growing points, the process not being essentially different from that by which peripheral, sectoral, or hyperchimeras arise.

The various types of these *Pelargonium* chimeras are familiar to horticulturists and have been propagated rather widely by cuttings, thus preserving quite uniformly the different forms. The periclinal chimeras having white peripheral cell layers are commonly cultivated forms on account of the striking effect of the white-margined leaves.

One of these varieties is known by the trade name of *Madame Salleroi*. During the summer of 1912 a plant of this type which was grown in an outdoor bed at the propagating houses of the New York Botanical Garden produced a branch in which the relative position of the two kinds of cells is reversed. When the cutting was made during the early part of the summer it possessed only leaves with the white margin. In October of that year, when first brought to the attention of the writer, the plant appeared as shown in the photograph here reproduced (see PLATE 20). Two branches, one the main and the other a lateral branch, bore leaves with the white cell layers placed externally to the green as was the case in the plant from which the cutting was made. The leaves were quite uniform in shape and in coloration and are quite typical for the variety known as *Madame Salleroi*. Dr. L. H. Bailey kindly made the varietal determination from leaves taken from these branches and further states in a letter to the writer that this variety has not been thus far placed specifically. As shown in PLATE 20, the enclosed green cells fail to develop uniformly toward the margin of the leaves, thereby leaving an irregular marginal zone of pure white cells. In the central portion of these leaves the enclosed green tissues show through the white.

On the third branch, which is a lateral one, the leaves are quite different. They are larger and the surface is green to the extreme margin. These leaves are not, however, of a uniform green, for through the central portion of each there is an irregular palmate-shaped area of lighter green which is due to white cell-layers enclosed between the upper and the lower green layers. In other words the place relationship of the white and the green cells is here reversed from what it is in the main part of the plant. In this branch the plant has literally turned itself inside out. Microscopical examination of free-hand sections confirmed the superficial observations as to the color relations.

In the black and white plate accompanying this article the general pattern in the leaves is well shown by the different shades. Since this plant has been under observation, about twenty leaves have matured on this branch. As shown in PLATE 20 the amount and distribution of the white tissue varies in the different leaves. In some leaves there are small flecks of white scattered through the green. A few of the leaves when about half developed show traces of a dark zonal band which is a feature of various showy-leaved Pelargoniums. When these leaves are mature, however, this zonal band is faint.

Baur notes a case of bud-variation identical with this one. He states (1909 *a*, p. 333), that the plant which he designated as Pel. 9 had white-bordered leaves but produced in 1908 a branch having wholly green leaves but which were plainly of a yellowish green in the center. The anatomical studies of these leaves (1909 *a*, p. 345) showed that the white cells were enclosed by the green cells.

In the light of Baur's anatomical studies this sort of bud-variation is readily understood as due to a mechanical readjustment of the two kinds of cells already in the growing points. This particular type involves more extensive rearrangement than the cases where pure green or pure white branches are produced by the development of a bud containing only one kind of cells to the exclusion of the other. For the development of a branch reversing the position of the two kinds of cells as described above there must be a breaking out of the enclosed green cells in the growing point and a growth of both green and white cells in such a manner that the green cells surround the white cells. It may be that in this case the green cells break forth at two separate points not far distant and that in further growth they meet, enclosing the white cells.

On the main portion of the plant here shown, the mature leaves possess over their whole surfaces two peripheral cell-layers that are white. To maintain this relationship the cell divisions which give rise to these layers must occur only in planes which are at right angles to the surface of the leaf. The outer layers do not contribute to the vascular tissues and the inner green tissue does not form epidermis, a fact clearly shown by Baur. In the sporting branch, however, the green cells get to the surface and form the epidermis as well as some of the mesophyl and vascular tissue, while the white cells cease to form epidermis and now contribute only to the inner tissues. The cells preserve the green and white character of their chromatophores but take on different structures or different functions according to position and environment.

In his interesting report of results of anatomical and hereditary studies of variegated varieties of *Pelargonium*, Baur was not especially concerned with the evidence of interaction between the two kinds of cells, the white and the green, where both exist in the same leaf. His photographs, however, show the same sort of difference which have appeared so strikingly in the case here under consideration.

The marked differences between the two kinds of leaves produced on this plant (PLATE 20) make it clear that the outer layers largely determine the size of the leaves and the depth of the lobing. When the green is outside the leaf is larger, more deeply lobed and like those which are borne on the branches that are composed purely of green tissue. When the white is outside, the leaf is much smaller and more like those leaves which are composed only of white tissue. Several plants of *Pelargonium Madame Salleroi* of the same clone as the plant producing this bud-variation have been under observation in the propagating houses. Several of these have produced leaves composed wholly of white cells. These have been of practically the same shape and size as the variegated leaves on the same plant. The pure white cells are, of course, dependent upon the green cells for carbohydrate food. In the case of a chimera relationship with the green cells enclosed, there may be mechanical and chemical stimuli to the overlying white cells that result in a slightly larger leaf. This effect is, however, not marked.

All the potentialities of a large and deeply lobed leaf are present in the green cells of a typical leaf of the *Madame Salleroi* variety. When these green cells get to the exterior those potentialities find expression, but as long as the peripheral layers of white are uniformly maintained, there is no visible evidence that these potentialities exist. Their suppression may be due chiefly to mechanical limitations imposed by the peripheral layers of white cells which decrease the number of cell divisions.

In the various plant chimeras there is an association of more or less independent and different kinds of cells. In the chimeras resulting from grafting, the two kinds of cells may be decidedly different, producing, when separate, two distinct types of leaves, but when associated together, forming leaves of still different patterns. The various chimeras produced by Winkler (1907 and 1909) and the chimera *Crataegomespilus Asnieresii* (see illustration by Baur 1911, *pl. VIII*) illustrate this phenomenon. In addition to such mechanical and physical interactions, Winkler (1910) has presented some evidence that there may be a vegetative fusion of cells in graft tissues producing what he would consider as the only true graft-hybrid, and he further holds that hybrid modifications may also result from the migration of such substances as atropin or nicotine between stock and scion.

These facts indicate that the general phenomena of plant chimeras have a very direct bearing on theories of morphogenesis and that cellular interaction is a potent factor in influencing cell differentiation and in determining the physical characteristics of such organs as leaves.

The bud-sports which arise from the various *Pelargonium* chimeras are, we may say, rather simple cases of variation due to a mechanical rearrangement of the kinds of cells already present. Their appearance is a confirmation of the rule that like produces like in its application to cell lineage rather than evidence of spontaneous somatic mutation or variation. In this case the real variation occurs when the white cells appear as the progeny of green cells. The frequency of this spontaneous variation in *Pelargonium* (and in other cases as well) and the real nature and the causes of the process are problems for future solution.

NEW YORK BOTANICAL GARDEN.

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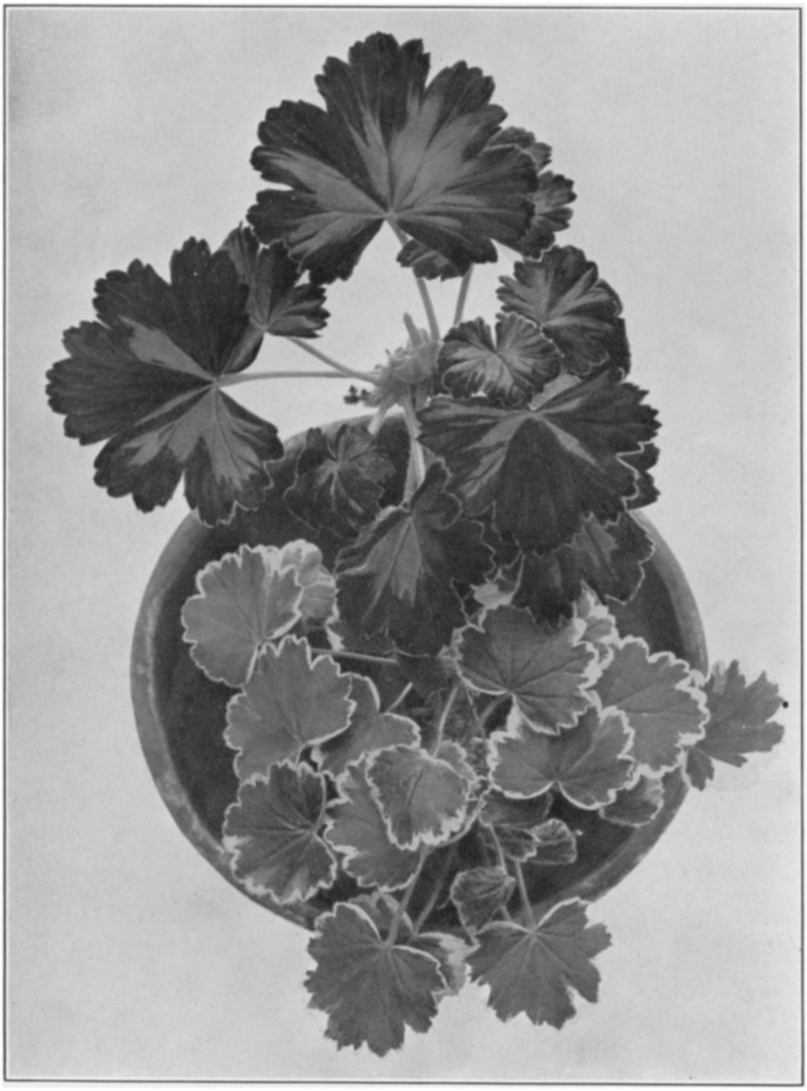

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